THE LATE GLACIAL AND HOLOCENE FLORA OF THE HUNGARIAN GREAT PLAIN

by

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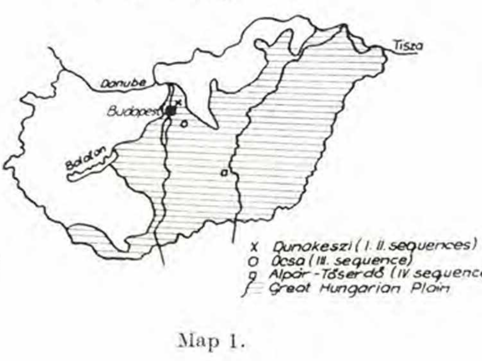
I. Introduction

Earlier research (S o ó 1926, 1929, 1931) on vegetational history utilizing the results of paleobotanical and palynological investigations carried out in Hungary and abroad, respectively, added considerably – even before starting palynological investigations in Hungary, – to the knowledge of the Quaternary vegetational development in the Hungarian Great Plain. The first pollen analytical investigations of lowlands were made by K i n t z l e r (1936). Following this, besides some individual analyses (G r e g u s s 1940; Z ó l y o m i 1946, 1953, 1958) palynological works made on lowland sequence have been published again only from the fifties (C s i n á d y 1954, 1959, 1960; J. B o r s y and Z. B o r s y 1955; V o z á r y 1957; I. M i h á l t z and M. M i h á l t z–F a r a g ó 1965). The sequences reported in the above publications originated from the northern region of the Hungarian Great Plain, situated beyond the river Tisza. On the basis of the results obtained in lowland palynological works

Position of sequences



Map 1.

Map 1.

and in the pollen analytical study of the bottom of the Lake Balaton (Zólyomi 1953), relying furthermore on macrofossil findings, some more papers on vegetational history were published (Soó 1940; Zólyomi 1953, 1958; Stieber, 1957).

Our own investigations were made in the central region of the Great Plain, situated between the rivers Danube and Tisza. In addition to the analysis of the Pleistocene strata (Járai-Komlódi 1966a, 1966c) in the work to be reported here, the palynological results of Holocene and Late-glacial sequences are presented. Of the four sequences outlined below sequences No. I. (Dunakeszi II) and No. II. (Dunakeszi I) date back to the Late-glacial period, sequences No. III. (Ócsa) and No. IV. (Alpár – Tőserdő) include the whole Holocene and new-Holocene layers, respectively (Map 1.).

II. Description of the Sites

1. Stratigraphy

The sequences are representing the replacements of the backwaters partly of the Danube (sequences I., II. and III.) partly of the Tisza (sequence IV.) filled up with diatomaceous lacustrian chalk (sequences I. and II.) and with plain moor-peat (sequences III. and IV.), in the bottom layers frequently fluvial silty sand.

Stratigraphic characteristics of the sequences

Sequence I., Dunakeszi II.
2,6 – 3,2 m diatomaceous gyttja
3,2 – 3,7 m sandy silt
3,7 – 4,4 m silty sand
4,4 – 4,8 m sand

Sequence II., Dunakeszi I.
0,0 – 0,1 m brownish oxidized peat
0,1 – 0,3 m plain moor-peat produced from sedge
0,3 – 2,7 m diatomaceous gyttja
2,7 – 2,9 m diatomaceous gyttja becoming sandy
2,9 – 3,5 m sandy silt
3,5 – 4,1 m silty sand

Sequence III., Ócsa
0,0 – 0,2 m black oxidized peat with snails
0,2 – 2,4 m plain moor-peat produced from sedge
2,4 – 2,7 m peaty clay
2,7 – 2,8 m sandy silt
2,8 – 3,0 m bluish fluvial sand

Sequence IV., Alpár-Tőserdő
0,0 – 3,8 m silty moor-peat produced from sedge

2. Climate and vegetation

The climate of the area under study (region between the Danube and the Tisza) is characterized by temperature warm, dry summers and severe winters, with a maximum of rain in summer.

The average temperature in January ranges from −1,4°C to −1,5°C, in July from 20,8°C to 21,6°C. One year's mean fluctuation is 22,3°C – 25,0°C. Yearly precipitation average is about 517 – 617 mm (50 years average).

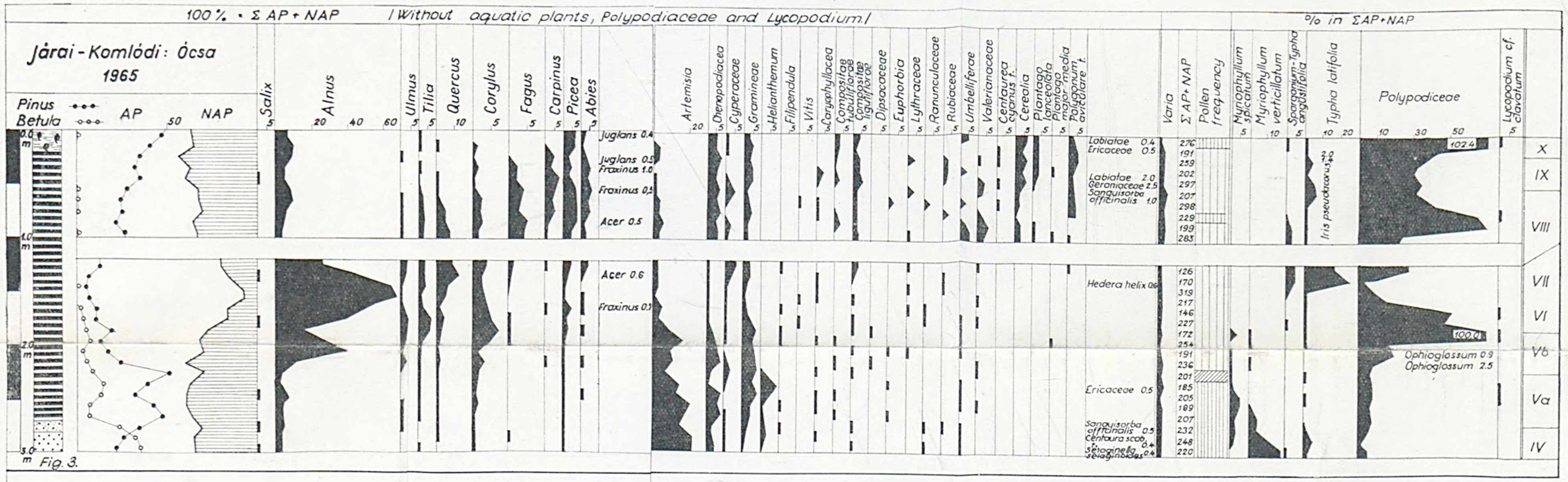
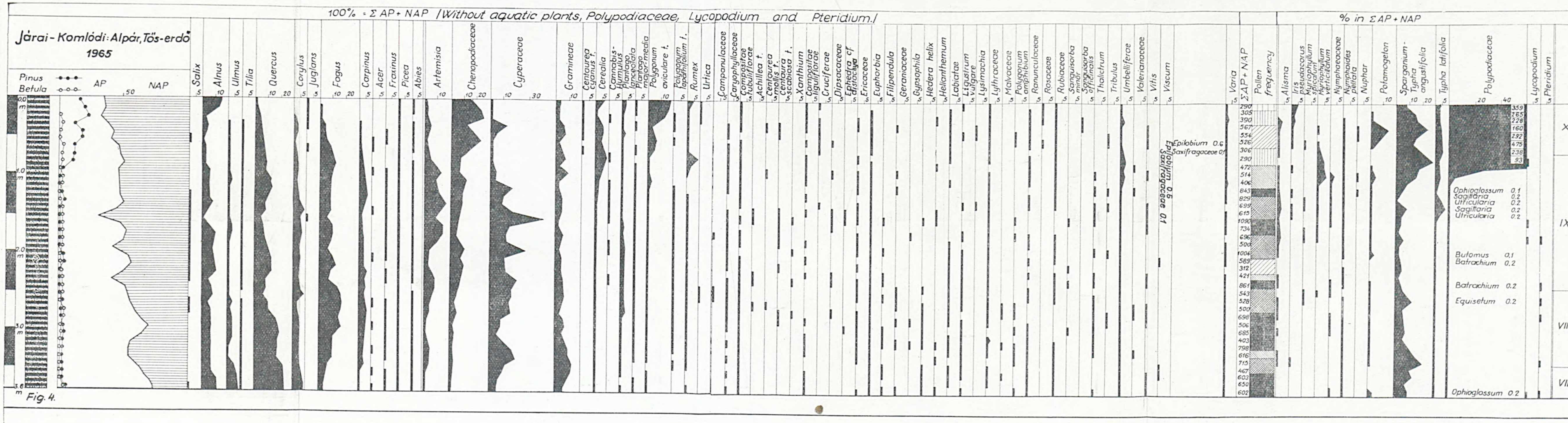
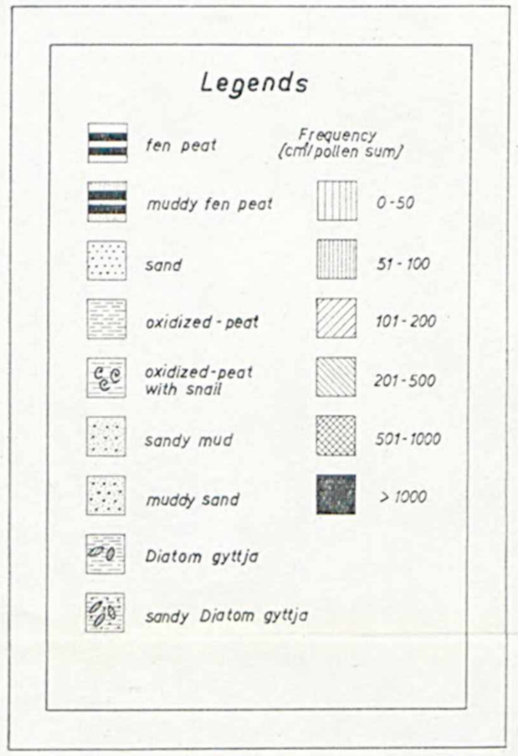
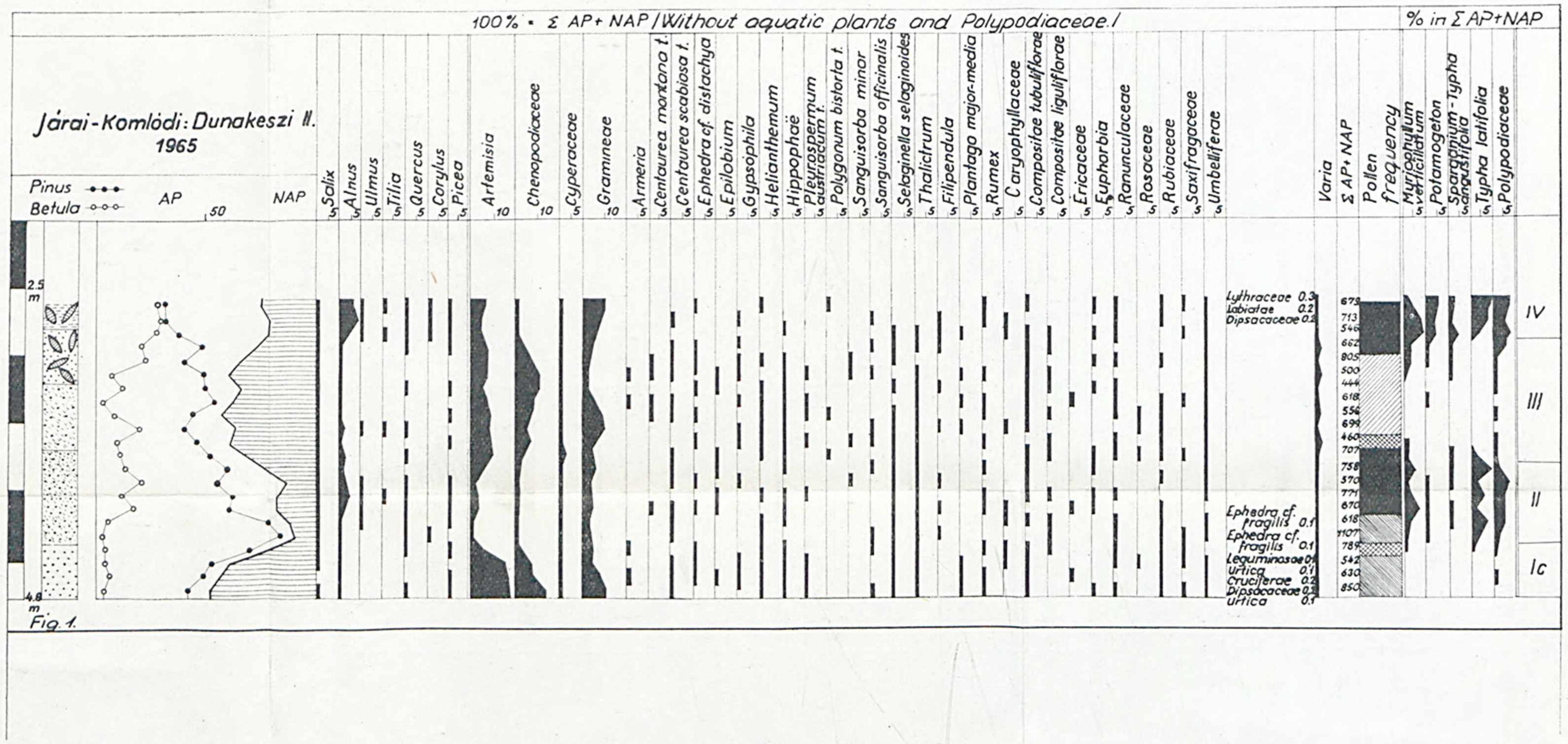

100% = Σ AP + NAP /Without aquatic plants, Polypodiaceae and Lycopodium/
% in Σ AP+NAP
Járai-Komlódi: Ócsa
1965
Pinus
Betula
AP
NAP
Salix
Alnus
Ulmus
Tilia
Quercus
Corylus
Fagus
Carpinus
Picea
Abies
Artemisia
Chenopodiacea
Cyperaceae
Gramineae
Helianthemum
Filipendula
Vitis
Caryophyllacea
Compositae
Dipsacaceae
Euphorbia
Lythraceae
Ranunculaceae
Rubiaceae
Umbelliferae
Valerianaceae
Centaurea cyanus t.
Cerealia
Plantago lanceolata
Plantago major-media
Polygonum aviculare t.
Varia
Σ AP+NAP
Pollen frequency
Myriophyllum spicatum
Myriophyllum verticillatum
Sparganium-Typha angustifolia
Typha latifolia
Polypodiaceae
Lycopodium cf. clavatum
Juglans 0.4
Juglans 0.5
Fraxinus 1.0
Fraxinus 0.5
Acer 0.5
Acer 0.6
Fraxinus 0.3
Labiatae 0.4
Ericaceae 0.5
Labiatae 2.0
Geraniaceae 2.5
Sanguisorba officinalis 1.0
Hedera helix 0.6
Ericaceae 0.5
Sanguisorba officinalis 0.5
Centaura scab. 0.4
Selaginella 0.4
Iris pseudacorus
Ophioglossum 0.9
Ophioglossum 2.5
X
IX
VIII
VII
VI
Vb
Va
IV
Fig. 3.

Fig. 3.


100% = Σ AP+ NAP /Without aquatic plants, Polypodiaceae, Lycopodium and Pteridium./
% in Σ AP+NAP
Járai-Komlódi: Alpár, Tős-erdő
1965
Pinus
Betula
AP
NAP
Salix
Alnus
Ulmus
Tilia
Quercus
Corylus
Juglans
Fagus
Carpinus
Acer
Fraxinus
Picea
Abies
Artemisia
Chenopodiaceae
Cyperaceae
Gramineae
Centaurea cyanus t.
Cerealia
Cannabis-Humulus
Plantago lanceolata
Plantago major-media
Polygonum aviculare t.
Polygonum lapathifolium t.
Rumex
Urtica
Campanulaceae
Caryophyllaceae
Compositae tubuliflorae
Achillea t.
Centaurea montana t.
Centaura scabiosa t.
Xanthium
Compositae liguliflorae
Cruciferae
Dipsacaceae
Ephedra cf. distachya
Ericaceae
Euphorbia
Filipendula
Geraniaceae
Gypsophila
Hedera helix
Helianthemum
Labiatae
Ligustrum vulgare
Lysimachia
Lythraceae
Malvaceae
Polygonum amphibium
Ranunculaceae
Rosaceae
Rubiaceae
Sanguisorba minor
Sanguisorba officinalis
Thalictrum
Tribulus
Umbelliferae
Valerianaceae
Vitis
Viscum
Epilobium 0.6
Saxifragaceae 0.1
Varia
Σ AP+NAP
Pollen frequency
Alisma
Iris pseudacorus
Myriophyllum spicatum
Myriophyllum verticillatum
Nymphaeaceae
Nymphoides peltata
Nuphar
Potamogeton
Sparganium-Typha angustifolia
Typha latifolia
Polypodiaceae
Lycopodium
Pteridium
Ophioglossum 0.1
Sagittaria 0.2
Utricularia 0.2
Sagittaria 0.2
Utricularia 0.2
Butomus 0.1
Batrachium 0.2
Batrachium 0.2
Equisetum 0.2
Ophioglossum 0.2
X
IX
VIII
VII
Fig. 4.

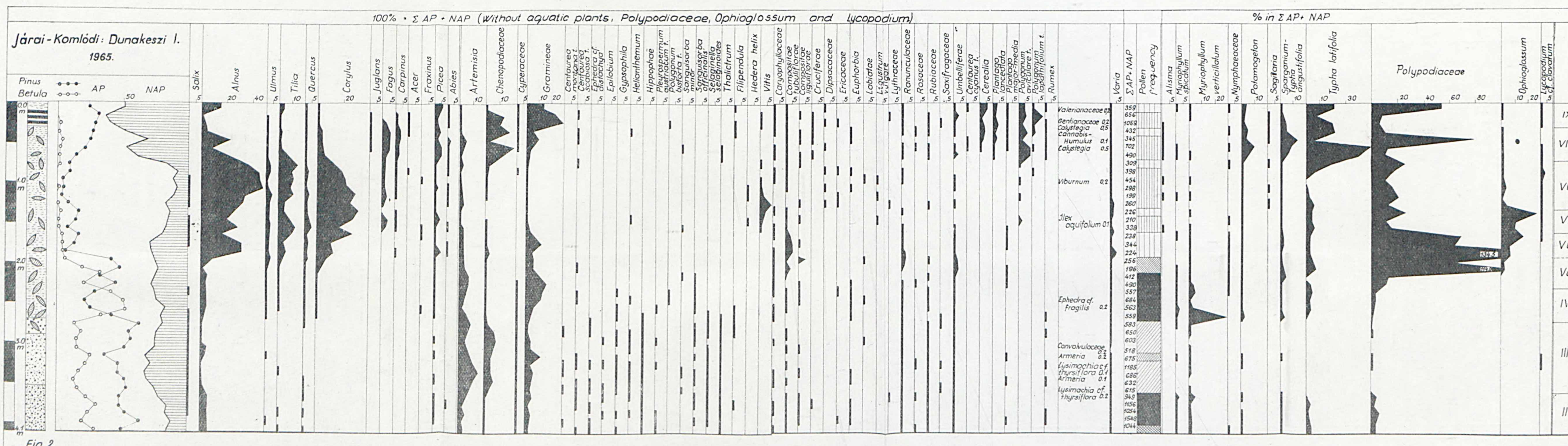


Legends
fen peat
muddy fen peat
sand
oxidized-peat
oxidized-peat with snail
sandy mud
muddy sand
Diatom gyttja
sandy Diatom gyttja
Frequency (cm/pollen sum)
0-50
51-100
101-200
201-500
501-1000
> 1000



100% = Σ AP+ NAP (Without aquatic plants and Polypodiaceae.)
% in Σ AP+NAP
Járai-Komlódi: Dunakeszi II.
1965
Pinus
Betula
AP
NAP
Salix
Alnus
Ulmus
Tilia
Quercus
Corylus
Picea
Artemisia
Chenopodiaceae
Cyperaceae
Gramineae
Armeria
Centaurea montana t.
Centaurea scabiosa t.
Ephedra cf. distachya
Epilobium
Gypsophila
Helianthemum
Hippophaë
Pleurospermum
Polygonum bistorta t.
Sanguisorba minor
Sanguisorba officinalis
Selaginella selaginoides
Thalictrum
Filipendula
Plantago major-media
Rumex
Caryophyllaceae
Compositae tubuliflorae
Compositae liguliflorae
Ericaceae
Euphorbia
Ranunculaceae
Rosaceae
Rubiaceae
Saxifragaceae
Umbelliferae
Varia
Σ AP+NAP
Pollen frequency
Myriophyllum verticillatum
Potamogeton
Sparganium-Typha angustifolia
Typha latifolia
Polypodiaceae
Lythraceae
Labiatae
Dipsacaceae
Ephedra cf. fragilis
Leguminosae
Urtica
Cruciferae
IV
III
II
Ic
Fig. 1.

Fig. 1.



100% = Σ AP + NAP (Without aquatic plants, Polypodiaceae, Ophioglossum and Lycopodium)
% in Σ AP+ NAP
Járai-Komlódi: Dunakeszi I.
1965.
Pinus
Betula
AP
NAP
Salix
Alnus
Ulmus
Tilia
Quercus
Corylus
Juglans
Fagus
Carpinus
Acer
Fraxinus
Picea
Abies
Artemisia
Chenopodiaceae
Cyperaceae
Gramineae
Epilobium
Gypsophila
Helianthemum
Hippophaë
Thalictrum
Filipendula
Hedera helix
Vitis
Caryophyllaceae
Cruciferae
Dipsacaceae
Euphorbia
Labiatae
Ligustrum vulgare
Lythraceae
Ranunculaceae
Rosaceae
Rubiaceae
Saxifragaceae
Umbelliferae
Cerealia
Rumex
Varia
Σ AP+ NAP
Pollen frequency
Alisma
Myriophyllum spicatum
Myriophyllum verticillatum
Nymphaeaceae
Potamogeton
Sagittaria
Sparganium-Typha angustifolia
Typha latifolia
Polypodiaceae
Ophioglossum
Lycopodium cf. clavatum
Valerianaceae
Gentianaceae
Calystegia
Cannabis-Humulus
Viburnum
Ilex aquifolium
Ephedra cf. fragilis
Convolvulaceae
Armeria
Lysimachia cf. thyrsiflora
IX
VIII
VII
VI
Vb
Va
IV
III
II
Fig. 2.

Fig.

Zonal forest association is represented by the oak forest steppe *(Convallario-Quercetum, Festuco-Quercetum, Aceri tatarico-Quercetum)*, at the present, however, this area with its surrounding is a cultivated land. The natural vegetation consists, for the most part, of azonal moor and gallery forests *(Carici-Alnetum pannonicum, Querco-Ulmetum hungaricum, Salicetum albae-fragilis)*, of adjacent high-grown sedgies *(Magnocaricion)*, reedies *(Phragmition)*, bog-meadows *(Agrostion albae)*, moor-meadows *(Caricion davallianae, Molinion coeruleae)* and of a rich aquatic vegetation *(Potametea)*.

III. Pollen analysis

1. Field and laboratory methods

Soil samples were taken with a spacing of ten centimeters by means of hand drills as used by geologists. Only the innermost, undisturbed parts of the samples were used for analysis. Materials to be tested were stored, after being soaked in a mixture of formalin and alcohol, in bottles sealed with paraffin.

The samples for pollen analysis were prepared by Erdtman's acetolysis method modified by Zólyomi (Zólyomi 1953). If necessary a hydrofluoric treatment (Erdtman 1943) was also applied.

The amounts of pollen found in the samples are represented in diagrams. The sum of tree (including *Corylus*) (AP) and herbaceous pollens (NAP) counted in a sample except those of hydrophytes and pteridophytes is taken as 100 per cent. The average per cent values of the taxa indicated for the different phases were calculated from the mean of the percentages of all samples analysed in the same phases of sequences. In some cases, in order to emphasize the changes which had occured in the grass vegetation some detailed diagrams are also given. Here the total of herbaceous plants (NAP) with the exception of the hydrophytes and pteridophytes is taken as 100 per cent. When indicating the different vegetational phases Firbas' pollen zone classification has been followed (1949, 1954).

2. Pollen zones

A) Dryas II (Older Dryas, pollen zone I*c*.)

Sequence I (Fig. 1.).

It has been supposed that at the bottom of sequence I zone I*c* is represented although it does not seem to be proved. This assumption could be admitted only by working up a series of complete Late-glacial sequences (demonstration of the Bölling interstadial). There is no doubt that the vegetational picture found in this zone differs very much from that of the Alleröd interstadial which is located above it and also from the one of the Pleni-glacial stage B demostrated in the region between the Danube and the Tisza (Járai-Komlódi 1966*a*, 1966*c*). At any rate this zone represents a transition between the Pleni-glacial B and the Alleröd. The character of the vegetation suggests a climate colder than that of the Alleröd interstadial, on the other hand in comparison with the Pleni-glacial stage B, there is a clear indication as to the improvement of the climate. Consequently in contrast with the dry, cold and treeless vegetation of the Pleni-glacial B, the occurence of trees, principally that of *Pinus* (54,5%) becomes characteristic even if at a subordinate level. The presence of *Betula* (6,1%), *Salix, Alnus, Quercus* and *Picea* was also established. No pollens of *Betula nana* or of dwarf willow type were found unlike in the Pleni-glacial A from the region between the Danube and the Tisza (J á r a i-K o m l ó d i 1966*a*, 1966*c*). This suggests a climate all the more favourable. The last stage of the Early-Weichselian period (end of the Brörup interstadial) and the Late-glacial phases proved to be very similar in their vegetational feature.

The average amount of the tree pollens was 62,5 per cent, the pollen of thermophilous trees occured in a very small quantity, not more than 2,8 per cent of the total of tree pollen. *Quercus* pollen is regarded as being secondary.

In the herbaceous vegetation *Artemisia* (13,9%), *Chenopodiaceae* (8,1%) and *Gramineae* (7,3%) prevailed, indicating on extensive Late-glacial open vegetation rich in species: such as *Armeria, Ephedra* cf. *distachya, Epilobium, Gypsophila, Helianthemum, Hippophaë, Pleurospermum austriacum, Sanguisorba officinalis, Selaginella selaginoides, Thalictrum, Plantago major-media. Rumex,* etc.

When the components of the Late-glacial open vegetation are expressed as the percentage of NAP the following peaks are obtained: *Artemisia* 40% (average 36,8%), *Chenopodiaceae* 30% (average 20,5%), *Gramineae* 25% (average 20,0%), Late-glacial steppe elements 13% (average 8,8%), other elements characteristic of Late-glacial open vegetation 10% (average 4,8%) as shown in Fig. 5. No pollens of aquatic plants were present, pteridophyta spores occured scarcely.

B) Alleröd (pollen zone II)

Sequences I and II (Fig. 1., 2.).

The border between the Dryas II. (I. c.) and the Alleröd was drawn where the value for NAP began to show a sudden decrease (from 45% to 8,0%, sequences I), the hydrophytes appeared and the pteridophytes became abundant.

Of the tree pollens showing an occurrence of about 85 per cent *Pinus* and *Betula* were dominant, *Alnus* was characteristic. The amount of other tree pollens *(Salix, Ulmus, Tilia, Quercus, Corylus, Picea, Abies)* is negligible. The treeless areas were reduced, the rates of herbaceous components to each other altered. The open vegetation remained very rich in species. Expressed as percentages of NAP the following rates of occurrence were established: *Artemisia* 20,5% (maximum 26%), *Chenopodiaceae* 8,6% (maximum 14%), *Gramineae* 29,4% (maximum 35%), Late-glacial steppe elements 4,4% (maximum 6%), other elements characteristic of Late-glacial open vegetation 6,6% (maximum 11%) (Fig. 5. and 6.). Pollens of six kinds of hydrophytes were demonstrated: *Typha latifolia, Potamogeton, Nymphaeaceae, Sparganium, Myriophyllum verticillatum, M. spicatum.* The spreading of all these, but especially that of *T. latifolia* indicates a more favourable climate as compared to that of the preceding phase. In addition to the increase in the amount of tree pollen there was also a decrease of certain heliophytes *(Ephedra, Gypsophila)* which points to reforestation. Among the herbs the pollens of some different dicotyledonous families occurred with a greater share, too. It is probable that within these families the shade tolarent or demanding taxa requiring a milder climate became widely distributed. That may also be the reason why *Gramineae* became here relatively more frequent than in the Dryas phases, i.e. they are including much more shade tolerant or demanding species than those included either in *Chenopodiaceae* or *Artemisia*.

C) Dryas III (Younger Dryas, pollen zone III)

Sequences I and II (Fig. 1., 2.).

The transition between the Alleröd and Dryas III is shown by the vegetational feature as compared with the preceding phase. This indicates a deterioration of the climate. The tree pollens showed a gradual but distinct diminishing, and the proportions represented by individual herbs have been altered. The number of the Late-glacial steppe heliophytes, as compared to those in Alleröd, shows a conspicuous increase. Their values related to the sum of NAP are: *Artemisia* 28,8% (maximum 47%), *Chenopodiaceae* 21,8% (maximum 39%), *Gramineae* 18,3% (maximum 30%), Late-glacial steppe elements 10,8% (maximum 20%), other species characteristic of Late-glacial open vegetation 5,8% (maximum 10%) (Fig. 5. and 6.).

The decrease of the tree pollens is a quantitative one, as the pollens of all the trees – with the exception of *Corylus* and *Abies* – which were present in the Alleröd could be demonstrated in this phase as well. The prevailing trees were *Pinus* and *Betula* here, too.

D) Pre-Boreal (pollen zone IV)

Sequences I, II and III (Fig. 1., 2., 3.).

The border between the Late-glacial period and the Holocene is indicated by the spread of the tree vegetation, especially by the sharp rise of *Betula*. The thermophilous broad-leaved trees also increased gradually.

Of the Late-glacial and Holocene phases the Pre-Boreal is the only one, where the number of *Betula* considerably exceeds that of *Pinus* and where at the same time, *Betula* reaches its absolute peak (52%). The proportion of thermophilous trees related to the total of tree pollen was 10,5% and from this phase most thermophilous trees *(Corylus, Quercus, Tilia, Ulmus)* form continuous curves.

Within the general decrease of NAP the fall is highly expressed for the heliophilous steppe plants and the characteristic Late-glacial herbs and so are the extinction of other ones and the gradually increasing value of *Gramineae*.

The average proportions expressed in the percentage of NAP are the following: *Artemisia* 32,8%, *Chenopodiaceae* 5,6%, *Gramineae* 32,1%, species characteristic of the Late-glacial open vegetation 6,3%.

The amelioration in climate at the beginning of the Holocene is also indicated by the aquatic plants. It was from this phase onwards that most of these plants showed a continuous and some of them a widespreading curve e.g. *Typha latifolia*, *Myriophyllum verticillatum* and *Polypodiaceae*.

E) Boreal (pollen sub-zones V.a and V.b)

Sequences II and III (Fig. 2., 3.).

The border between Pre-Boreal and Boreal was marked by a sharp and definitive fall of Betula and a sudden rise of *Pinus* and a gradual one of *Corylus*. The whole Boreal phase is characterized by the high proportion of herbaceous plants (30,3% on the average). Boreal can be devided into two sub-zones, the border of which was drawn at the intersection of *Pinus* and *Corylus* curves.

Sub-zone V.a is characterized by the high value of *Pinus* (42,1%) and by the slow increase of the curves of *Corylus*, *Alnus* and mixed oak forest species. In the herbaceous vegetation the following rates of occurrence, expressed in the percentage of NAP are worth noting: *Artemisia* 32,2% (maximum 53%), *Chenopodiaceae* 11,4% (maximum 25%), *Gramineae* 27,5% (maximum 60%) and *Helianthemum* 5,7% (maximum 26%).

The V.b sub-zone is characterized by the sudden drop in *Pinus*, by the first peaks of *Corylus* and *Alnus*, by the simultaneous spread of mixed oak forest species, and by the appearance of *Carpinus*. In the open vegetation *Artemisia* and *Gramineae* showed a certain decrease (to 25,6% and 25,1%, respectively), *Helianthemum* disappeared entirely and other dicotyledonous families e.g. *Compositae* (10,4%), *Umbelliferae* (4,2%) gained in importance.

F) Atlantic (pollen zones VI and VII)

Sequences II, III and IV (Fig. 2., 3., 4.).

The Atlantic-Boreal border has been established where the extension of *Alnus*, *Tilia*, *Quercus* and the diminishing to a minimum of *Artemisia* and *Chenopodiaceae* met. All *Alnus* and mixed oak forest species were culminating in the Atlantic. *Corylus* remained characteristic to the same extent as in the Boreal. Next to *Carpinus* the beech appeared.

The usual division into two parts of the Atlantic phase was possible in sequence II. In sequence III the low pollen frequency did not provide any opportunity for a reliable separation. As to sequence IV, only the younger stage of the Atlantic was represented. In sequence II mixed oak forest species showed a similar behaviour in both Atlantic phases, however, in the older phase (VI) *Corylus* had an expending tendency. In the younger stage *Corylus* was slowly decreasing, *Alnus* reaches its peak, *Pinus* and *Betula* practically disappeared, it was in that phase that AP culminated.

The Boreal steppe disappeared, *Artemisia*, *Chenopodiaceae*, other dicotyledonous heliophilous steppe plants were replaced by forests with herbaceous forest plants belonging to different families, with shrubs (e.g. *Viburnum*, *Ligustrum)* and with some significant indicators, such as *Vitis*, *Hedera*, *Viscum*, *Ilex* (Fig. 2., 4., 8.), of a mild, wet and warm climate of the Atlantic period.

G) Sub-Boreal (pollen zone VIII)

Sequences II, III and IV (Fig. 2., 3., 4.).

The border between the Sub-Boreal and the Atlantic has been drawn partly by the spreading of the plants indicating a change of climate into a more humid and cooler one *(Fagus, Carpinus, Picea,* aquatic plants), partly by the appearance of the influence of human activity in the vegetational change.

A general decrease in the AP value (60,8%) can be seen in the diagrams. The participation of *Fagus* and *Carpinus* was increasing and, with exception of sequence IV, *Picea* showed a rising tendency, too. Expressed in total pollen percentage the values are: *Carpinus* 4,7%, *Picea* 3,1%, *Fagus* 10,4%, the latter having reached its maximum. The share of *Alnus*, and that of the mixed forest diminished *(Alnus* 8,4%, *Quercus* 8,9%, *Tilia* 1,6%, *Ulmus* 1,5%). The values of *Pinus* (12,9%), and *Betula* (2,7%) also rose slowly.

In the open vegetation *Artemisia* (8,9%), *Chenopodiaceae* (15,3%) became important again, somewhat significant were *Gramineae* (16,3% in sequence II) and *Cyperaceae* (33,0% in sequence IV). Weeds and cultivated plants *(Centaura cyanus* tip., *Plantago lanceolata* tip., *Polygonum aviculare* tip., *Rumex, Urtica, Cannabis-Humulus, Cerealia)* with an average value of 17,5% calculated in NAP % also appeared or spread. As compared to the Atlantic, the participation of climatic optimum plants diminished from 9,3% to 0,3% (calculated in NAP %).

H) Sub-Atlantic and present time (pollen zones IX and X)

Sequences II, III and IV (Fig. 2., 3., 4.).

In the course of these investigations the most detailed picture of the vegetational changes in the Sub-Atlantic could be observed in the 1,8 thick successive layers with high pollen frequency of sequence IV. Each corresponding layer, however, found in the three sequences shows a similarity in its main characteristics.

The Sub-Boreal-Sub-Atlantic border has been drawn where a newer large-scale rise of weeds and cultivated plants and a sudden ascent of the *Pinus* curve could be observed.

In this phase *Fagus* was slowly diminishing, it even disappeared. The number of *Carpinus* first had a tendency to rise (sequences III and IV) then gradually diminished till the end of the phase. Diminishing followed by the extinction of *Fagus* and *Carpinus* may be due to climatic influences characterized by a more continental and dryer pattern. The diminishing of mixed oak forest species, the spread of *Artemisia, Chenopodiaceae, Gramineae,* cultivated plants and weeds may be attributed to human activity. The rise in the number of *Pinus* pollen may be a result of longdistance transport by wind to the increased treeless localities.

The climate of present time does not differ from the Sub-Atlantic one. Present time vegetation would sooner reflect a more intensive human activity as it is shown first of all by the composition of the anemophilous herbaceous vegetation. As indicated in Fig. 9. the proportion in NAP of pioneer plants, mainly heliophilous species belonging to *Artemisia* and *Gramineae* and of cultivated plants and weeds *(Cerealia, Centaura cyanus, Cannabis, Plantago, Polygonum, Rumex, Urtica* species) is different in the phases IX and X. In the Sub-Atlantic the former, in zone X the latter prevailed. A probable cause of this phenomenon may be the fact that human activity appeared first (phases VIII, IX) in the form of deforestation (for "land occupation") which favoured

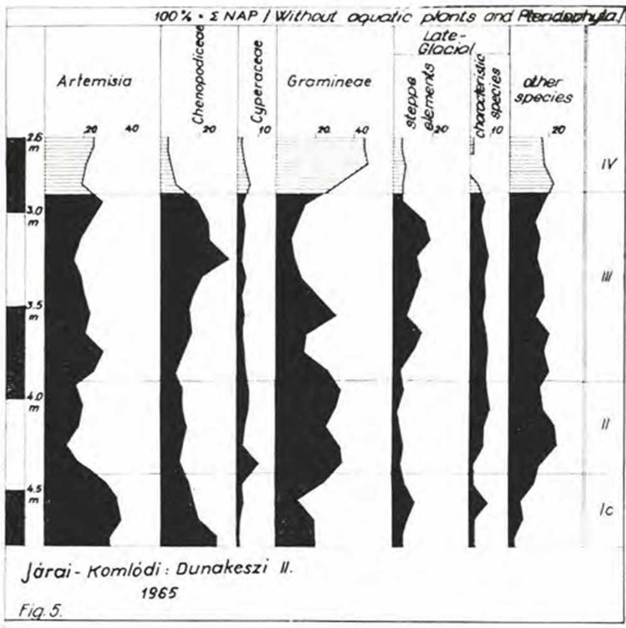

100% = Σ NAP / Without aquatic plants and Pteridophyta /
Late-Glacial
Artemisia
Chenopodiceae
Cyperaceae
Gramineae
steppe elements
characteristic species
other species
2.6 m
3.0 m
3.5 m
4.0 m
4.5 m
IV
III
II
Ic
Járai-Komlódi: Dunakeszi II.
1965
Fig. 5.

Fig. 5.

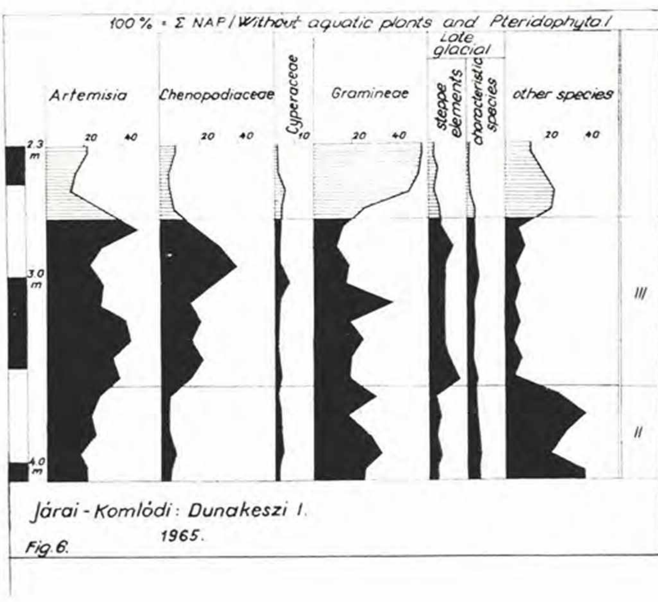

100% = Σ NAP / Without aquatic plants and Pteridophyta /
Late glacial
Artemisia
Chenopodiaceae
Cyperaceae
Gramineae
steppe elements
characteristic species
other species
2.3 m
3.0 m
4.0 m
III
II
Járai-Komlódi: Dunakeszi I.
1965.
Fig. 6.

Fig. 6.

the spread of pioneer heliophytes and later (phase X in the form of agriculture which resulted in the predominance of cultivated plants and weeds. The accumulation of *Chenopodiaceae* during phase X might be explained as well by the spreading of weeds belonging to this family.

IV. Discussion

Reforestation – The cold treeless semi-desert loess-steppe vegetation grown during the Last Glaciation (Pleniglacial *B)* in the region between the Danube and Tisza rivers became gradually reforested in the course of the Late-glacial period. Its beginning could not be established in this work and the earliest forest development could not be followed continuously, as sequence I, is supposed to start from the end of Dryas II only. The Alleröd as well as the Dryas phases preceding and following it was demonstrated from the Great Plain geologically, too. In agreement with the results obtained hitherto in Europe the Dryas III loess layer has been found, by C^{14} dating to be $10 \cdot 480 \pm 1200$ years old (Kriván 1960). The Bölling vegetation as well as the climatic and vegetational changes which had set in at the boundary of the Pleniglacial B and the Late-glacial period continue to remain unknown. Further palynological investigations concerning the Great Plain are needed to elucidate the full vegetational development in the Late-glacial and the detailed division of this period for the zones peculiar to Europe.

In the phases demonstrated from the Late-glacial period the most important role in reforestation was played in the region studied by *Betula* and *Pinus* species. *Alnus* and *Salix* were also of considerable importance. The role of the thermophilous broad-leaved trees is much more uncertain. The amount of their pollens is very low, their curve is continuous only from the Holocene on. The AP average in Dryas II is 62,4%, the proportion of the thermophilous broad-leaved tree pollens (*Alnus* always included) calculated on the sum of AP is not more than 2,8%. In the Alleröd, with 85 per cent of AP, it is only 6,5%, in the Dryas III, with 69% of AP it is 2,7% only. The value of the thermophilous broad-leaved tree pollens reaches 10,5% in the Pre-Boreal, from here their curve becomes continuous and rises steadily.

According to the results of charcoal analysis broad-leaved tree forests existed in Hungarian Central Mountains, during the Late-glacial period. *Quercus* is even supposed to have been able to survive the Last Glaciation and to remain in existence as a preglacial (Eem interglacial) relic (Stieber 1957). Their occurrence on the Great Plain is much more problematic. Several factors such as the rate of reforestation, the considerable quantity of *Typha latifolia* bound to the July 14°C isotherm, the appearance of *Nymphaeaceae* lead us to believe that the climate – at least that of the Alleröd – could have suited the thermophilous trees on the Great Plain, too, especially at its margins where these sequences were taken from. On the basis of such considerations the thermophilous tree pollens can be supposed to be of a primary nature and so the forests – in this area – in Alleröd may be compared with a southern type pine-birch taiga already admixed with broad-leaved trees described from the western part of the Soviet Union, the so-called European taiga (Berg 1958).

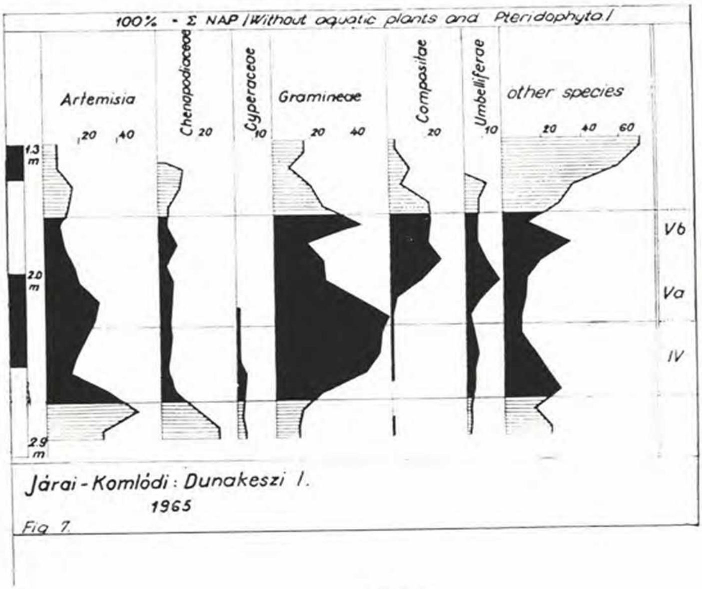

100% = Σ NAP /Without aquatic plants and Pteridophyta/
Artemisia
Chenopodiaceae
Cyperaceae
Gramineae
Compositae
Umbelliferae
other species
1.3 m
2.0 m
2.9 m
Vb
Va
IV
Járai-Komlódi : Dunakeszi I.
1965
Fig 7.

Fig. 7.

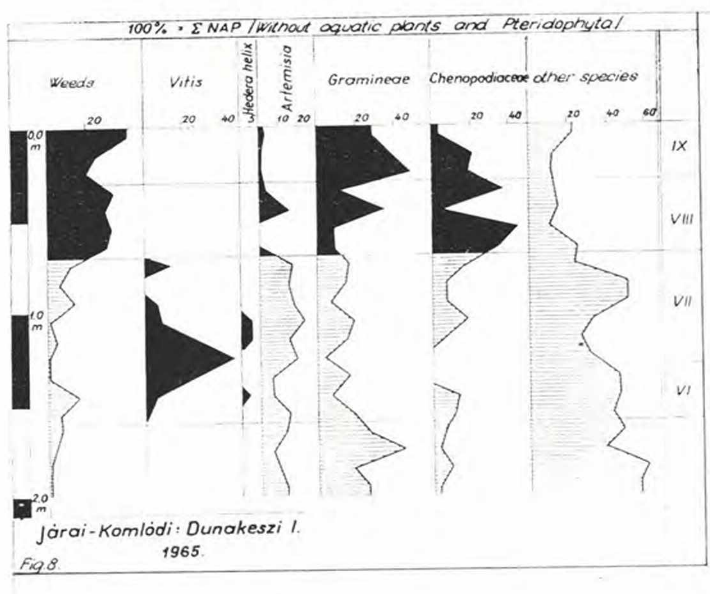

100% = Σ NAP /Without aquatic plants and Pteridophyta/
Weeds
Vitis
Hedera helix
Artemisia
Gramineae
Chenopodiaceae
other species
0.0 m
1.0 m
2.0 m
IX
VIII
VII
VI
Járai-Komlódi : Dunakeszi I.
1965
Fig.8.

Fig. 8.

However, because of the very low proportion of the thermophilous trees these pollens are best regarded as being of a secondary nature, derived from the surrounding highlands by longdistance transport. According to this assumption, during the Late-glacial period they could not have any important role in the vegetation of the Great Plain, even in the case of favourable climatic conditions. The widespread distribution of *Pinus* and *Betula* and their competition might have been the main inhibiting factors of the immigration of thermophilous trees.

Betula. – In the Late-glacial period the curves of *Betula* show repeated rises to a higher or lesser extent (sequences I and II), however, these were not so important and did never exceed the *Pinus* values. On the contrary, in the Pre-Boreal *Betula* had spread suddenly and widely in general with maximum values, considerably exceeding even the curves of *Pinus*. This is a conspicuous phenomenon occurring in all our sequences containing Pre-Boreal layers (I, II, III) and is in agreement with the dominance of *Betula* in the Pre-Boreal layers from the Yugoslav Deliblat lowland which pertains geographically to the Great Plain (Gigov and Bogdanovic 1962). This can be found also in a number of sequences both in Hungary and in neighbouring countries (Kintzler 1936; Gigov 1956; Ralska-Jasiewiczowa 1966). Besides then there are many examples pointing to a rapid spread of tree-birches *(B. pendula, B. pubescens)* in an area which had been covered partially by pine-birch forests during the Late-glacial interstadials and the beginning of Holocene, under the influence of a climatic amelioration. This climatic change favoured the spread of *Pinus (P. silvestris)*, too, *Betula*, however, having been more of a pioneer tree, its growth was speedier, its seed production aerlier and superior. Consequently it was able to immigrate much more quickly into treeless areas. It can be supposed, therefore, that the peaks of *Betula* dated by certain authors from the very end of Dryas III (J. Borsy and Z. Borsy 1955; Csinády 1960) or from the beginning of the Boreal (Krippel 1965) may have pertained to the Preboreal.

In the Late-glacial sequences examined no pollens of dwarf birch *(Betula nana* tip.) were found, only those of tree-birches *(Betula alba* tip.)

Characteristics of the Late-glacial herbaceous vegetation. – The Late glacial herbaceous vegetation of the Great Plain was rich in species and had a curious mixed composition, similarly to those of Western and Northern Europe (Iversen 1954; Godwin 1956; Florschütz 1958; Wasylikowa 1964). Here, heliophilous *Chenopodiaceae*, *Artemisia* species and *Gramineae* were the prevailing grass components, in addition, however, some other steppe elements such as *Centaurea scabiosa* tip., *C. montana* tip., *Gypsophila* cf. *fastigiata*, *Ephedra* cf. *distachya*, *Ephedra* cf. *fragilis*, *Plantago major-media*, *P. maritima* tip., *Helianthemum*, *Armeria maritima*, *Sanguisorba minor* also occurred. The rest of the vegetation consisted of elements which at present inhabit dunes *(Hippophaë)*, of arctic-alpine species *(Selaginella selaginoides)*, of plants of high mountain meadows *(Polygonum bistorta)*, of alpine-boreal species *(Pleurospermum austriacum)*, of members of tall herb meadows and of bog, marsh vegetations *(Sanguisorba officinalis, Rumex, Thalictrum, Epilobium-Chamaenerion)*. These so-called "characteristic elements of the Late-glacial

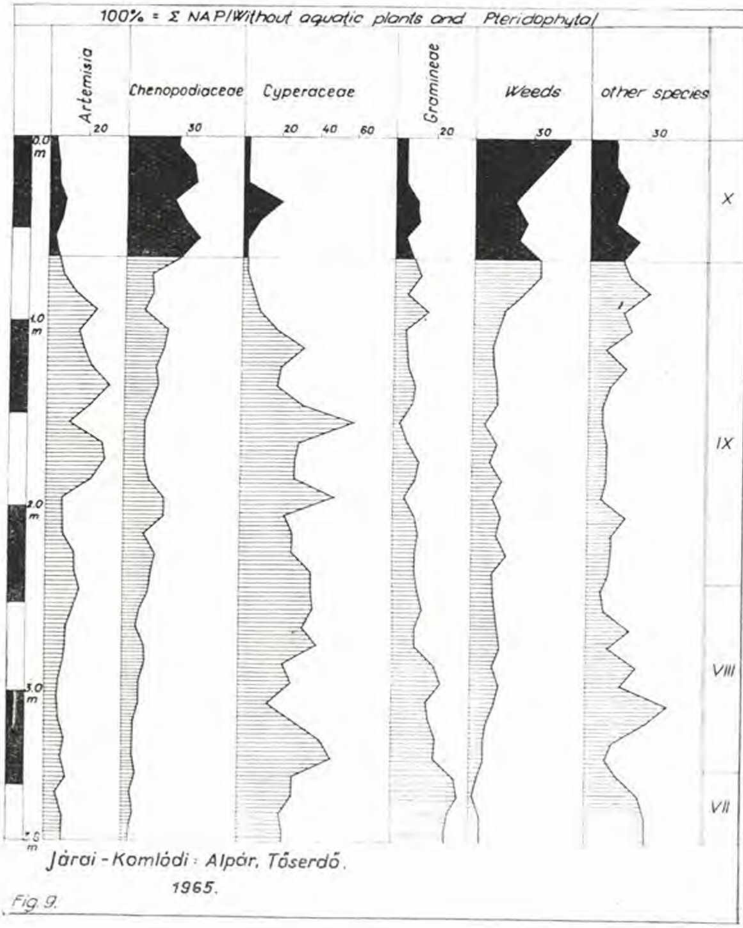


Fig. 9.

open vegetation" disappeared on the Great Plain, after the Late-glacial period, in general as early as the Pre-Boreal.

According to Iversen the mixed character of the Late-glacial herbaceous vegetation could be attributed partly to the fact that among the climatic factors light conditions must have been very favourable to the heliophilous steppe plants as well as to the heliophilous arctic-alpine species. From the distribution in Hungary of some plants the conclusion can be drawn that they were mainly warm and dry demanding species, for many of them, however, light had to be a more decisive factor. So for example the European habitats of *Ephedra* occur at present, under very warm climatic conditions, but they can also be found in Siberia, beyond the Arctic Circle and in the Alpine region of Tibet. Similarly, *Hippophaë* grow not only on dunes but also in subalpine regions and so does *Armeria maritima* (Gams 1943; Iversen 1954; Godwin 1954; Walter 1954).

Another possible reason for this mixed character of the flora is that the edaphic conditions of Late-glacial had been very favourable to pioneer plants differing in ecological requirement. This resulted in the fact that they had immigrated and spread together (I v e r s e n 1954).

A q u a t i c p l a n t s. – When the vegetation of a certain area is to be characterized pollens of waterplants can not be regarded as deriving from true local species. However, their identification is necessary and is of importance all the more because the behaviour immigration, extinction, spread of certain species may be of great help in determining the climatic conditions of different phases. The majority of them are known to be cosmopolitan because of the compensatory influence of water. Therefore, the results have to be interpreted with precaution. It has been confirmed by several authors (S z a f e r 1954; I v e r s e n 1954, 1964; W a s y l i k o w a 1964; W e s t 1964) that in many cases aquatic plants are none the less more valuable indicators of the temperature conditions than terrestrial plants are. In certain respects they are even superior to the latter. For example in the case of an amelioration in temperature they react more promptly than do the terrastial plants and in consequence of their distribution speed they will quickly spread. This feature appears e.g. the sequence I, at the beginning of Alleröd (Fig. 1.) where the spread of *Typha latifolia* preceds the peak of *Betula*. Most aquatic plants behave like pioneers and by finding ideal conditions in the water, after their immigration begin to spread immediately. If it comes to a temperature decrease during an unfavourable period they survive by help of their resistant organs and by the next amelioration of the climate they will soon recgain their reproductive capacity. In water there is less competition than e.g. in the case of heliophytes and forests, and so these disturbing factors can be eliminated. However, even in the presence of all these advantages only those aquatic plants can be taken into consideration which occured in deposits of eutrophic waters and whose distribution is not limited by edaphic factors e.g. by the lime content of water. Such reliable aquatic plants are e.g. *Nymphaea, Nuphar, Potagometon natans, Typha latifolia, Myriophyllum verticillatum* (S a m u e l s s o n 1934; S o ó and J á v o r k a 1951; I v e r s e n 1954; S z a f e r 1954).

S t e p p e v e g e t a t i o n. – On the examined areas one may follow in broad outlines the alterations in the composition of the open vegetation which had occurred during the Late-glacial (Dryas II, Dryas III), Pre-Boreal and Boreal phases.

The Late-glacial cold, continental steppes were in the first place composed of *Artemisia, Chenopodiaceae* and some *Gramineae*. In their grasses the presence of other steppe heliophytes is also of importance e.g. that of *Ephedrae, Gypsophila* cf. *fastigiata, Armeria maritima, Helianthemum, Sanguisorba minor*, and that of plants of sub-artic meadows *(Selaginella selaginoides)*.

On the Pre-Boreal steppe the number of *Chenopodiaceae* and that of the heliophylous steppe plants characteristic of the Late-glacial diminish. *Artemisia* remains important further on, though from the sequences including also the Late-glacial layers (Sequences I., II) one may see that its average value as compared to that of the Dryas phases decreased by 8%, while that of *Gramineae* showed a tendency to increase. *Selaginella, Armeria* disappeared but some cold requiring, shade tolerant alpine-boreal species, e.g. *Pleurospermum* cf. *austriacum* could still be demonstrated. In this phase the plant community characterizing a cold continental steppe had already become almost entirely extinct, the species had changed and had given place to the warm continental steppe.

From the open vegetation of the Boreal phase the plants characteristic of the Late-glacial steppes, the sub-arctic, alpine-boreal species had disappeared completely. A grass vegetation rich in *Gramineae* had been prevailing, in all probability *Festuca-Stipa* herbs (S o ó 1959), with a number of Dicotyledons especially from the *Compositae* and *Umbelliferae* families (Fig. 7.). *Artemisia* is a significant component of Boreal steppes as well. As it is known, during this phase there was a warm, dry climate favourable to the accumulation of alkaline salts. The earliest Post-glacial sodic soils are supposed to have originated from this time (S o ó 1959). On these sodic soils the bulk of the different *Artemisia* species could have grown, as they do today. In sequence III *Chenopodiaceae* and, at least in the first half of the Boreal, also *Helianthemum* are characteristic sporadically. Of course, during this phase several warm requiring *Artemisia*, *Chenopodiaceae* and *Helianthemum* species, other than those of the Late-glacial period might have existed. It is worth mentioning that from the European territory of the Soviet Union wide steppes also consisting of *Artemisia* and *Chenopodiaceae* (NAP value over 40%) were recorded (L i s s i z i n a 1953).

Steppe as climax vegetation in the Boreal. – S o ó was the first to assume the existence on the Hungarian Great Plain of the last climax steppe dating far back to the Boreal period (S o ó 1929). This statement was later accepted and supported by Z ó l y o m i with the reservation that "to have a full evidence congruent data obtained by further borings should be necessary" (Z ó l y o m i 1953). According to W e n d e l b e r g e r, during the Boreal phase a forest steppe vegetation had been prevailing on the Hungarian Great Plain and the last primeval steppe vegetation was established on its steppe spots (W e n d e l b e r g e r 1954, 1956). Comparing our results with those obtained by Z ó l y o m i on the Lake Balaton they are found to be fairly congruent. Reckoned as a percentage of total pollen Z ó l y o m i (1953) has reported for the Boreal an average NAP value of 38,2% (maximum 40%), whereas in sequences II and III from the Great Plain this value was found to be 30.3% (maximum 40%). This cogruency is striking, the comparison seems, however, not to be quite reliable. The diagram from Lake Balaton does not indicate separately the number of local aquatics, so it can be supposed that the number of "varia" and the sum of NAP is fallacious. In addition to that in Z ó l y o m i's calculations the frequency of herbaceous pollen was related to that of AP, and the high percentage of NAP (90%) obtained was taken as an indication of the existence of Boreal climax steppe.

In the Holocene and Late-glacial phases preceding the Boreal the studied area of the Great Plain was never found to be entirely reforested. In the Dryas phases, even in the Pre-Boreal, there were fairly large areas covered with a treeless steppe vegetation as it has recently been supposed by Z ó l y o m i and S o ó (Z ó l y o m i 1958, 1964; S o ó 1959). Though the full vegetational history of the Late-glacial is unknown (Bölling, Dryas I), it is very likely that in some regions of the Great Plain many steppe areas have remained treeless from the Brörup interstadial or probably from the last interglacial to the very end of the Boreal phase. The cold loess steppes of the glacials diminished, but possibly continued to exist during the Dryas phases. They even might have transmitted certain species with wider ecological demands and received some newer species which had appeared upon the amelioration of climate. Little by little its flora became changed, and in the Boreal the cold loess steppe was replaced by the warm continental steppe.

There is no doubt in the studied areas wooded vegetation has also existed. Part of *Betula* can be supposed to have been *B. pubescens* grown in the moors as local species. Part of *Pinus* pollens could have originated through long distance transport. Nevertheless, as the climax steppe zone of the Soviet Union is penetreted by forest steppe tongues at some sandy sites so may have subsisted forest steppe spots in certain areas of the Hungarian Great Plain (e.g. in the neighbourhood of the Danube), too, as indicated in these diagrams. Consequently, in the first half of the Boreal phase (V.a), besides sandy and sodic steppes with grasses and *Artemisia* an oriental type of *Pinus silvestris* forest steppe with oaks, limes and hazels might have existed. In the second half of the Boreal (V.b) *Pinus* disappeared, and a mixed oak forest steppe rich in hazels might have remained characteristic. As the *Tilia* pollens present in a considerable amount proved to pertain to the *Tilia cordata* tip. (P r a g l o w s k i 1962) these forest steppes may have been most similar to *Dictamno-Tilietum cordatae* (F e k e t e 1965) in the plant communities of Hungary.

As far as the Boreal climax steppe is concerned these investigations contributed mainly to the study of the steppe composition by determining the herbaceous pollens. For a definit demonstration of the existence of the climax steppe in Boreal, pollen analyses of additional Holocene sequences originating from the middle part of the Great Plain and from the areas beyond the river Tisza would be necessary. As these sequences apply almost exclusively to territories along the Danube, we think that the demonstration of forest steppe in the Boreal does not deny, the existence of climax steppe in the Great Plain as a whole.

S u b - z o n e s t h e B o r e a l p h a s e, C o r y l u s. – Similarly to other authors (J e s s e n 1935; F i r b a s 1949; J ö r g e n s e n 1954; F i r b a s and R o c h o w 1956; F i r b a s, M ü n n i c h, W i t t k e 1958; K l a u s 1961; S z c z e p a n e k 1961) the Boreal has been divided into two sub-zones. The border between them was established on the basis of the reciprocal behaviour of *Pinus* and *Corylus* (sequences II and III), respectively.

According to F i r b a s the Central European forest development in the Boreal was characterized by a widespread distribution of *Corylus* mainly in the west and on highlands, and by the spreading of *Pinus* in the regions where forests rich in *Betula* had been dominating in the Pre-Boreal. Sub-zone V.a is a period abounding in *Pinus* with a marked *Pinus* peak, a period where *Corylus* had shown a tendency to increase, and mixed oak forests and *Alnus* were insignificant. In sub-zone V.b the number of *Pinus* and in some localities even that of *Corylus* were diminishing while *Quercetum* mixtum and *Alnus* were increasing (F i r b a s 1949 p. 312.).

On the basis of Firbas' statements and of the results already obtained (e.g. Firbas and Rochow 1956; Klaus 1961; Krippel 1965; Járai-Komlódi 1966b) it can be concluded, that in the early Boreal (V.a) *Pinus* forests or forest steppes may have been fairly expanded in Central Europe. Also the markedly high values of pine in the diagrams presented may allow the conclusion that in certain localities of the Great Plain *Pinus* forests existed still at the beginning of the Boreal.

The basic aspect of the pattern of the Central European Boreal forest development described by Firbas has also been confirmed by these analyses in that the two sub-zones of Boreal can be characterized by vegetations rich in *Pinus* and in hazel, respectively. With regard to the general behaviour of *Corylus*, however, certain divergences have been found. So the hazel proportion as shown by most of the diagrams referring to Hungary – chiefly to the lowlands (Kintzler 1936; Zólyomi 1953; Csinády 1954, 1960; J. Borsy and Z. Borsy 1955) – was, even in a period rich in hazel, much lower than that in the northern and western regions of this country, especially in mountainous and hilly areas. This may be the reason why some authors in interpreting the diagrams referring to the Hungarian Great Plain presumed the absence of the Boreal period from the sequences and tried to explain this by climatic causes (dry, warm periods) (Csinády 1954, 1955; J. Borsy and Z. Borsy 1955).

The relatively low frequency of *Corylus* even during the period rich in hazel can be explained by assuming that the dry, warm climate of Boreal prevailing on the Great Plain was not favourable for the spreading of hazel. Another divergence in the behaviour of *Corylus* is that in this country the curves of hazel do not decrease at the end of the Boreal, show even in the Atlantic phase values similar to those of the Boreal and will have diminished only at the end of the Atlantic period. The climate of the Atlantic may have been the best for hazel. Its distribution on a larger scale was hampered, however, on account of its high light requirement – presumably by the widespread broad-leaved forests (Járai-Komlódi 1968).

Indicators of the climatic optimum: Viscum, Hedera, Ilex, Vitis. – Since the publication in 1944 of Iversen's paper several authors have published standard works on the role of *Viscum*, *Hedera* and *Ilex* as climatic indicators (Iversen 1944; Mikkelsen 1949; Godwin 1956; Troels-Smith 1960). Their importance is emphasized by their demand on a high temperature, precipitation and mild climate which was characteristic of the Holocene climatic optimum and appeared in Europe earliest in the Atlantic phase. The appearence of these indicators is an immediate sign of setting in of this climatic change.

In the Atlantic phase their pollens have been found in many European localities, though their frequency was always very low and expressible but in thousandths as a rule.

To the three plants mentioned above *Vitis* might still be added, however, its pollen has rarely been demonstrated, in general only in the later (Sub-Boreal, Sub-Atlantic) periods. From the Atlantic phase it was found south of Hungary, e.g. in Italy (Beug 1964). In the sequences studied by us the pollens of all the four plants were found in the Atlantic phase. *Hedera* and *Vitis* were found in three borings (sequences II, III and IV), *Viscum* only in the Atlanti cphase of sequence IV, *Ilex* only in that of sequence II.

Hedera is an Atlantic-mediterranean plant (S o ó and J á v o r k a 1951). It is less sensitive to the summer temperature but for its spreading it requires a relatively high average winter temperature not lower than – 1,5°C even in the coldest month (I v e r s e n 1944).

Viscum is an Eurasian flora element (S o ó and J á v o r k a 1951). In the case of a relatively high summer average temperature (above 16–17°C) it is able to tolerate a lower winter temperature (even –6°C).

Vitis silvestris is a lowland, Ponto-mediterranean element (S o ó and J á v o r k a 1951) with a temperature requirement similar to that of *Viscum* (T r o e l s - S m i t h 1960). Its area is determined by an annual average temperature of 9–21°C. A July average temperature exceeding 28°C it does not spread (P á l i n k á s 1955; K o z m a 1964).

The sensitivity of *Ilex* to continental climatic conditions is higher than that of any of the three species mentioned above. Only a mild, rainy climate is favourable to it. It is an Atlantic-mediterranean element, unable to tolerate any extremities (W a l t e r 1954), and even in the Mediterranean area occurs only in countries abundant in rain.

Vitis, *Viscum*, *Hedera* are native plants in this country even today. *Ilex* is supposed to be extinct because of an unfavourable climatic change which had taken place after the Atlantic phase. Even today it is not an indigenous plant of the Hungarian flora. Its appearance is regarded to be important in the Atlantic not only because it indicates for the Atlantic a more favourable climate than that of our days but also because the thorough investigation of its actual spreading conditions makes it possible to get a more exact estimation of the Atlantic climate (J á r a i - K o m l ó d i 1967).

Vitis is also a significant plant having a greater pollen frequency in these sequences than in other countries. It is supposed that during the Atlantic period is had been widely spread. Its appearance and spread by that time could have been related not as much to a rise in the temperature but rather to an increase in humidity, and to its migration conditions.

The presence of *Vitis silvestris* is characteristic of park forests. Its high frequency in the Atlantic may be in connection, to some extent, with the distribution of park forests (high percentage of *Alnus). Vitis* is today in Hungary a characteristic species of *Fraxino pannonicae-Ulmetum* hardwood parklands of the Great Plain (S i m o n 1957; S o ó 1957, 1958). Together with similar Slovenian communities as opposed to those in Central Europe it is a common differential species of the South Eastern European hardwood parklands (S o ó 1958, 1964). Today it is no more a common plant. It was, however, as shown by earlier authors much more expanded as late as the last century not only in parklands, but also in the broad-leaved tree forests of the Hungarian Central Mountains and in those of the Great Plain as well (K e r n e r 1863; F e i c h- t i n g e r 1899; D e g e n 1901). This plant is very likely to have been extirpated from the mountain and lowland forests, or forced back into the riverside park forests by a climate turning dry, then by the "land occupation" of man and finally by some parasites (T e r p ó 1962).

Human activity. – According to archeological and paleontological records man's deforesting and shepherding activity affecting the vegetation first appeared at the boundary between the Atlantic and Sub-Boreal phases, about 5000 years ago. For that very reason it seems to be quite difficult to mark a natural boundary which would be due to the effect of a climatic change, which had taken place on the border between Atlantic and Sub-Boreal. It is necessary, however, to differentiate between climatic changes and human activity as possible factors influencing the events.

In all European countries where palynological investigations of the Holocene vegetational history led to the interpretation of delicate details, this question was the subject of intensive research (e.g. Jessen 1938; Iversen 1941; Faegri 1940; Godwin 1956; van Zeit 1959; Morrison 1959; Troels-Smith 1960; Koperowa 1962; Smith 1961; Turner 1962, 1964).

In the elucidation of this problem in addition to tree pollens the appearance and behaviour of weeds, cultivated plants and climatic optimum indicators are also of importance. In these sequences the increase of *Fagus* and *Carpinus* pollens shows a change to a colder and more wet climate. This is indicated by a rich aquatic vegetation as well and also by a descrease of the thermophilous broad-leaved trees *(Ulmus, Tilia, Quercus).* The increasing tendency of *Pinus* is likely to be a result of its long distance transport into treeless regions. However, the diminishing of the reforested areas caused any more by the climatic conditions but by the clearance. This can be concluded from the increase in the curves of *Betula* on the one hand and of weed and cultivated plants on the other.

Betula is a pioneer tree probably indicating the beginning of the reforestation of an area and the first steps of a natural succession. This happened more than once during the Early Weichselian and Late-glacial periods and at the beginning of Holocene. Whenever another increase in the spread of *Betula* is observed, in a land already forested it will indicate a retrogression in the development of the vegetation. This is very often caused by clearance, burning of forests and soil degradation connected with it. However, it can be brought about also a natural degradation of the soil e.g. in consequence of an alteration in the climate or groundwater level. An increase in *Betula* curves of a similar nature appears in the Sub-Boreal and Sub-Atlantic phases of several pollen diagrams of Hungary (Zólyomi 1931; Kintzler 1936; Vozáry 1957; Csinády 1959). The accumulation of weeds and Cerealia reveals a shepherding and land cultivating activity.

All these results are in agreement with the data hitherto recorded on the Sub-Boreal climate of Hungary (Zólyomi 1958; Soó 1959). Accordingly, the climate in the Sub-Boreal should have been cooler and wetter than that which most probably existed in the Atlantic. This, however, does not exclude an accidental appearance of drier periods of shorter duration (diminishing of *Alnus)* such as have previously been pointed out (Vozáry 1957). In spite of a favourable climate the forested regions found in the studied areas of the Great Plain were diminished. This may perhaps be attributed to the activity of the deforesting, shepherding man. As an identification of the climatic optimum plants and weeds is missing from the Holocene palynological works published so far in Hungary, the number of these sequences is not sufficient to draw any general conclusions and therefore no attampt will be made to discuss the matter in detail. In order to get some more detailed informations about the Sub-Boreal climate and the Atlantic-Sub-Boreal boundary a palynological analysis of much more Holocene sequences is needed.

Climatic data. – The alterations which had occurred in the climate of Holocene have been suggested by a number of Hungarian authors to be in agreement with the results obtained for Central Europe. Our conclusions support this view and give some new informations about certain details (Járai-Komlódi 1968). As to the climatic changes during the Late-glacial phases very little has been known so far. Our conclusions concerning this problem will be reported elsewhere (Járai-Komlódi 1968). Here only a brief summary will be given. Though soil humidity may have been favourable in general including Hungary, yet, the degree of humidity on the Great Plain especially in the stadials, must have been lower than in the European regions situated to the north and west of Hungary. This is demonstrated by the steppes rich in heliophytes (many *Artemisia*, *Ephedra*, *Gypsophila*, etc.) and by the scarcity of chionophilous plants.

The climate of Dryas II is far from being well known because of the incompleteness of the analysed sequence only a single layer was available. The pollens of severel plants present in Dryas III are still missing here, and the less forested land also indicates that the climate in Dryas II was colder than in Dryas III.

In the Alleröd, the occurrence of *Pleurospermum austriacum* together with *Typha latifolia* and *Nymphaea* as well as the feature of the tree vegetation suggest that the average temperature of July amounted to about 17°C to 18°C, and that of January to about −2°C to −4°C.

From the presence of *Armeria maritima* and *Pleurospermum austriacum* in Dryas III, from the extinction of *Typha latifolia* and on the basis of the feature of tree vegetation it can be assumed that the average temperature of January was about −4°C to −6°C, and that of July about 13°C to 14°C.

V. Summary

A palynological analysis of Late-glacial and Holocene layers from the Great Hungarian Plain and from the region between the rivers Danube and Tisza is presented.

It seems to be a striking resemblance between the flora of the Late-glacial periods and that of the end of Brörup interstadial reported elsewhere (Járai-Komlódi 1966c).

In the Late-glacial period the tree vegetation consisted of a pine-birch parkland, and the grass vegetation abounding in species was formed by heliophilous steppe plants.

In moister areas moor vegetation comprising arctic-alpine, alpine-boreal species was formed.

In the Alleröd phase the climate seems to have been suitable for the establishment of thermophibus broad-leaved trees in the areas investigated. The low frequency of their pollens, however, indicates that they were rather of a secondary nature.

A high dominance of tree-shaped *Betula* (in all probability *B. pendula, B. pubescens)* is characteristic of the forests of the Pre-Boreal phase.

As to the behaviour of the plants prevailing in the steppe vegetation the following changes were found: in the case of Late-glacial steppes *Artemisia, Chenopodiaceae, Gramineae* and other heliophytes were most characteristic. In the Pre-Boreal steppes *Chenopodiaceae* and other heliophytes diminished, *Artemisia* remained important, and *Gramineae* gained in importance. In the Boreal grasses *Gramineae* rich in Dicotyledons *(Umbelliferae, Compositeae)* were most characteristic, *Artemisia*, in some localities also *Chenopodiaceae* and *Helianthemum* remained important whereas other plants characteristic of the Late-glacial steppes disappeared.

In the older Boreal sub-phase (V.a) an oriental type of *Pinus silvestris* forest steppe with oaks, limes and hazels was demonstrated and in the younger sub-phase (V.b) a mixed oak forest steppe rich in hazels and limes. The participation of hazel, even during the periods rich in hazels was found to be much less than indicated by the diagrams from mountainous regions or by those from the northern most or western most territories of Europe. The Boreal climate was not favourable to its spread on the Great Plain. At the end of the Boreal it did not become less and showed a similar frequency even during the Atlantic in consequence of the prevailing climatic conditions supposed to have been highly favourable to its existance. Its further spread might have been hampered by the broad-leaved tree forests, then, under the influence of climatic change at the end of the Atlantic its frequency became diminished. In this time a mixed oak forest steppe is supposed to have come into prominence as a dominant tree vegetation.

Besides *Viscum, Hedera* and *Ilex* a considerable amount of *Vitis* turned up from the Atlantic phase. Of these four plants *Ilex* does not grow any more spontaneously in Hungary.

The influence of human activity upon the vegetation appeared from the beginning of the Sub-Boreal phase in a decrease of forests on the one hand, and in the appearence and gradual spread of weed and cultivated plants on the other hand. Apart from the cultural influence, the cool and humide climate of the Sub-Boreal period brought about a closing of oak forests, and a spread of *Carpinus* and *Fagus*.

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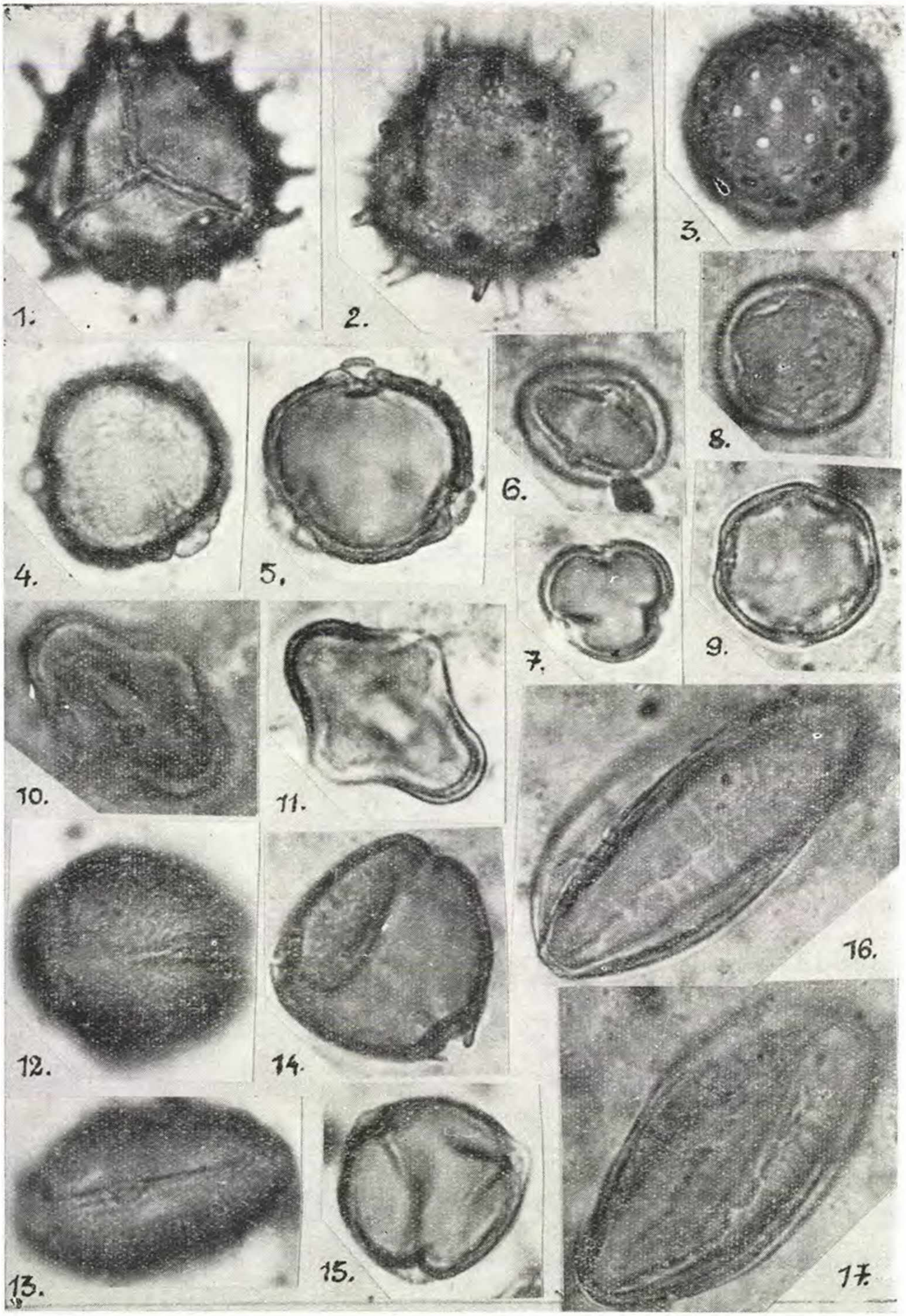

Plate I. 1 – 2. *Selaginella selaginoides*, 3. *Chenopodiaceae*, 4 – 5. *Sanguisorba minor*, 6 – 7. *Filipendula* sp., 8 – 9. *Thalictrum* sp., 10 – 11. *Pleurospermum austriacum* type, 12 – 13. *Helianthemum* sp., 14 – 15. *Hippophaë rhamnoides*, 16 – 17. *Ephedra* cf. *distachya*. Enlargement ×1000

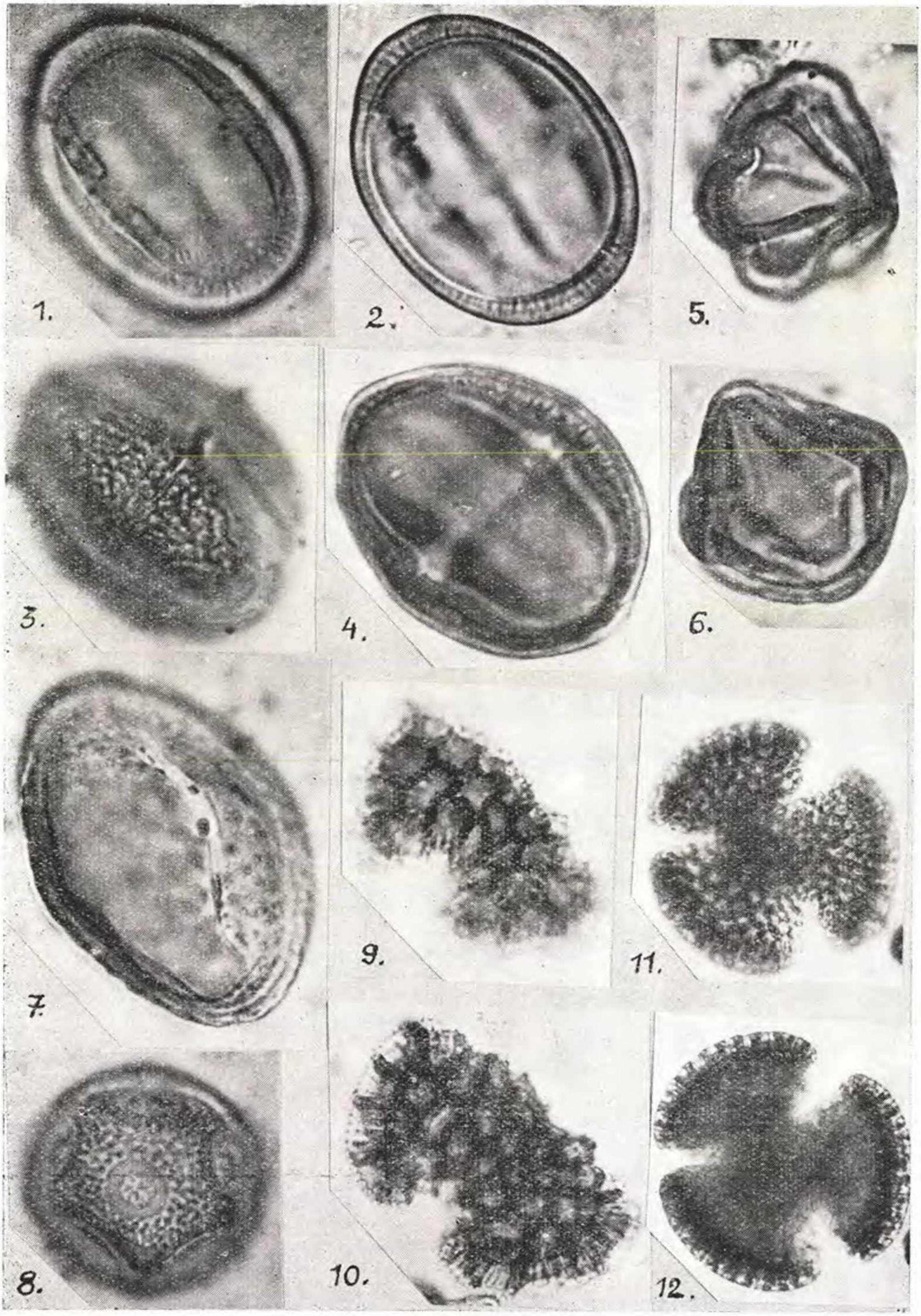

Plate II. 1 – 2. *Polygonum bistorta* type ×1000, 3 – 4. *Centaurea montana* type ×1000, 5 – 6. *Sanguisorba officinalis* ×1000, 7. *Centaurea scabiosa* type ×1000, 8. *Gypsophila* cf. *fastigiata* ×1000, 9 – 10. *Armeria maritima* type A ×500, 11 – 12. *Armeria maritima* type B. ×500

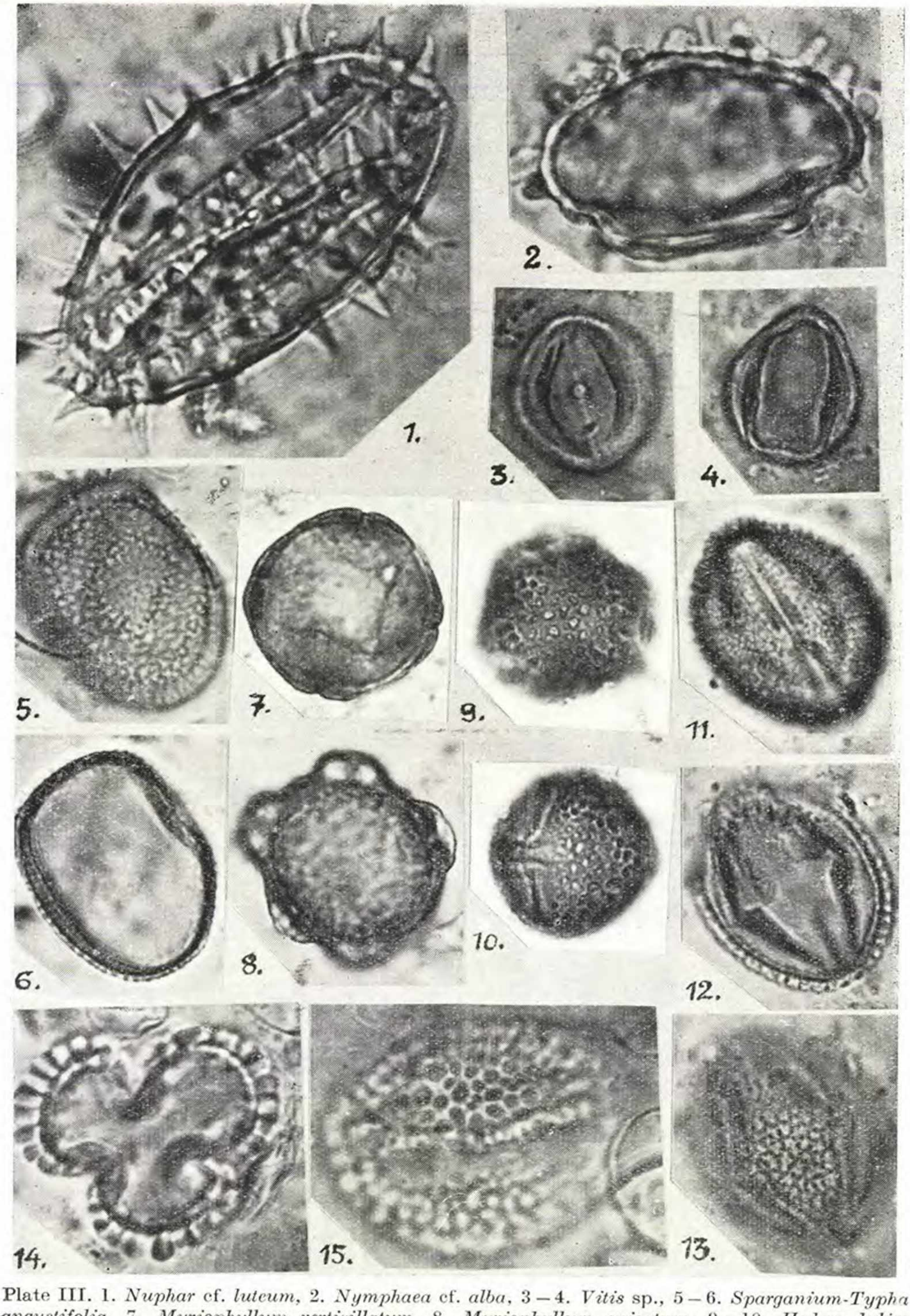

Plate III. 1. *Nuphar* cf. *luteum*, 2. *Nymphaea* cf. *alba*, 3 – 4. *Vitis* sp., 5 – 6. *Sparganium-Typha angustifolia*, 7. *Myriophyllum verticillatum*, 8. *Myriophyllum spicatum*, 9 – 10. *Hedera helix*, 11 – 13. *Viburnum* sp. 14 – 15. *Ilex aquifolium*. Enlargement $\times 1000$

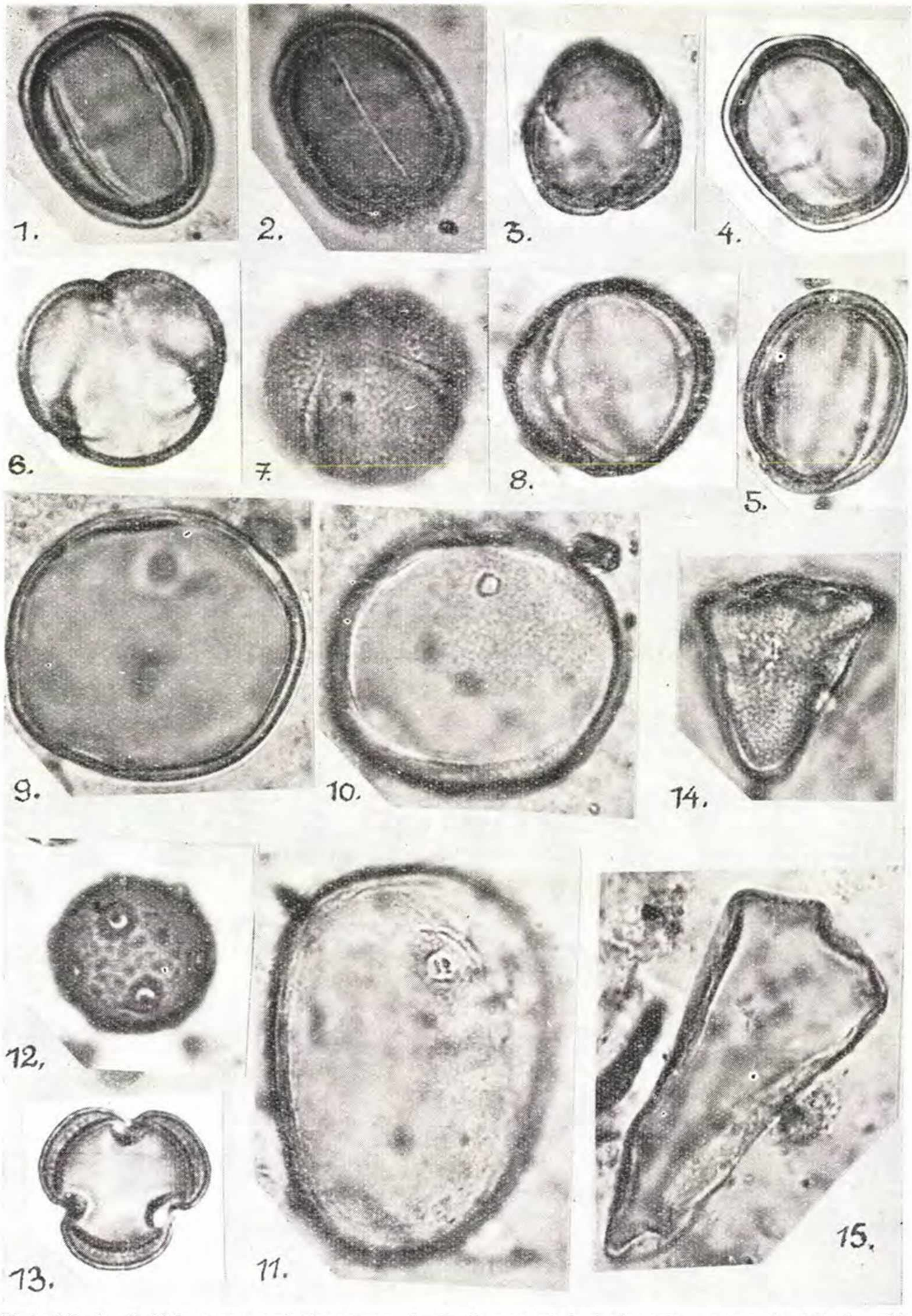

Plate IV. 1 – 5. *Polygonum aviculare* type, 6 – 8. *Rumex* cf. *hydrolapathum* type, 9 – 10. *Cerealia*, cf. *Triticum*, 11. *Cerealia*, cf. *Secale*, 12. *Plantago lanceolata*, 13. *Artemisia* sp. 14. *Cyperaceae* cf. *Carex* type, 15. *Cyperaceae* cf. *Scirpus* type. Enlargement ×1000

LITERATURE

Berg, L. S. 1958: Die geographischen Zonen der Sowjetunion I. Teubner Verlag, Leipzig.

Beug, H. J. 1964: Untersuchungen zur spät- und postglazialen Vegetationsgeschichte im Gardaseegebiet unter besonderer Berücksichtung der mediterranen Arten. Flora 154. 401–444.

Borsy, J., Borsy, Z. 1955: Pollenanalytische Untersuchungen im nördlichen Teil der Nyírség. Acta Univ. Debrecen 2. 271–280.

Csinády, G. 1954: A bátorligeti láp története a pollenanalízis tükrében. [The history of the bog Bátorliget on the basis of pollenanalysis]. Földr. Ért. 3. 684–690.

Csinády, G. 1959: A csarodai láposodott folyómeder pollenanalitikai vizsgálata. [Pollenanalytical study of the marshy river-bed of Csaroda.] Acta Univ. Debrecen 5. 271–278.

Csinády, G. 1960: A kokadi láp palinológiai vizsgálata. [Palynological study of the bog Kokad]. Acta Univ. Debrecen 6. 239–251.

Dégen, Á. 1901: Flora von Herculesbad. Budapest.

Erdtman, G. 1943: An Introduction to Pollen Analysis. Chronica Bot. Waltham.

Faegri, K. 1940: Quartärgeologische Untersuchungen im westlichen Norwegen II. Zur spätquartären Geschichte Jaerens. Bergens Mus. Arb. 1939–1940 Nat. r. No. 7.

Feichtinger, S. 1899: Esztergom megye és környékének flórája. [The flora of the county Esztergom and its environment]. Esztergom.

Fekete, G. 1965: Die Waldvegetation im Gödöllőer Hügelland. Akadenie Verlag, Budapest.

Firbas, F. 1949: Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen I. Fischer Verlag, Jena.

Firbas, F. 1954: Die Synchronisierung der mitteleuropäischen Pollendiagramme. Danm. Geol. Unders. II. R. No. 80, 12–21.

Firbas, F., Münnich, K. O., Wittke, W. 1958: C^{14}-Datierungen zur Gliederung der nacheiszeitlichen Waldentwicklung und zum Alter von Rekurrenzflächen im Fichtelgebirge. Flora 146. 512–520.

Firbas, F., von Rochow, M. 1956: Zur Geschichte der Moore und Wälder im Fichtelgebirge. Forstw. Cbl. 75. 367–380.

Florschütz, F. 1958: Steppen- und Salzsumpfelemente aus den Floren der letzten und vorletzten Eiszeit in den Niederlanden. Flora 146. 489–492.

Gams, H. 1943: Der Sanddorn (Hippophae rhamnoides L.) im Alpengebiet. Beih. Bot. Centralb. 62. 68–96.

Gigov, A. 1956: Bisherige Ergebnisse über die postglaziale Geschichte der Wälder Serbiens. Inst. Écol. Biogéogr., Rec. trav. 7. No. 3, 1–26.

Gigov, A., Bogdanovic, M. 1962: The genesis of the peat-bogs in the surroundings of latska Pescara. Arch. Sci. Biol. Beograd 14. 7–31.

Godwin, H. 1956: The History of the British Flora. University Press, Cambridge.

Greguss, P. 1940: A Szeged-öthalmi mammut- és szénlelet pollenanalitikai vizsgálata. [Pollenanalitical investigation connected with the fossils of mammoth and charcoal at Szeged and Öthalom]. Szegedi Városi Múzeum Kiadv. II. sor., 1–23.

Iversen, J. 1941: Land occupation in Denmark's stone age. Danm. Geol. Unders. II. R. No. 66., 1–68.

Iversen, J. 1944: Viscum, Hedera, and Ilex as climate indicators. Geol. Fören. Förh. 66. No. 3, 463–483.

Iversen, J. 1954: The Late Glacial flora of Denmark and its relation to climate and soil. Geol. Unders. II. R. No. 80, 87–119.

Iversen, J. 1964: Plant indicators of climate, soil, and other factors during the Quaternary. Rep. VIth INQUA, Warsaw, 1961, vol. II. 421–428.

Járai-Komlódi, M. 1966a: Palinológiai vizsgálatok a Magyar Alföldön a Würm glaciális és a holocén klíma- és vegetációtörténetére vonatkozóan. [Palynological investigations on the climatic changes and the vegetational history of the Great Hungarian Plain during the Würm glaciation and the Holocene]. Kandidátusi disszertáció, Budapest, 1–280. Manuscript.

Járai-Komlódi, M. 1966b: Adatok az Alföld negyedkori klíma- és vegetációtörténetéhez. I. A vegetáció változása a Würm glaciális és a holocén folyamán, palinológiai vizsgálatok alapján. [Quaternary climatic changes and vegetational history of the Great Hungarian Plain. I. Changes in the vegetation during the Würm glaciation and Holocene, as evidenced by palynological investigations]. Bot. Közl. 53. 191–201.

Járai-Komlódi, M. 1966c: Études palynologiques des couches de la dernière époque glaciaire (Brörup, Pléniglaciaire) de la Grande Plaine Hongroise. Pollen et Spores 8. 479–496.

Járai-Komlódi, M. 1968: Adatok az Alföld negyedkori klíma- és vegetációtörténetéhez. II. A klíma változása a Würm glaciális és a holocén folyamán, palinológiai vizsgálatok alapján. [Quaternary climatic changes and vegetational history of the Great Hungarian Plain. II. Climatic changes during the Würm glaciation and Holocene, as evidenced by palynological investigations]. Bot. Közl. 55. in press.

Jessen, K. 1935: Archaeological dating in the history of North Jutland's vegetation. Acta Arch. Kobenhavn 5. 185–214.

Jessen, K. 1938: Some West Baltic pollen diagrams. Quartär 1, Berlin.

Jörgensen, S. 1954: A pollen analytical dating of Maglemose finds from the bog Aamosen, Zealand. Danm. Geol. Unders. II. R. No. 80, 159–187.

Kerner, A. 1863: Das Planzenleben der Donauländer. Innsbruck.

Kintzler, O. 1936: Pollenanalytische Untersuchung von Mooren des westlichen pannonischen Beckens. Beih. Bot. Centralbl. 54. 515–546.

Klaus, W. 1961: Pollendiagramme der Moore des niederösterreichischen Waldviertels II. Das Schremser Moor (Schwazinger Torfstich). Verh. geol. Bundesanst. 1961. 128–132.

Koperowa, W. 1962: The history of the Late Glacial and Holocene vegetation in Nowy Targ Basin. Acta Palaeobot. 2. 1–66.

Kozma, P. 1964: Szőlőtermelés I. [Ampelology]. Mezőgazdasági Kiadó, Budapest.

Krippel, E. 1965: Die Rekonstruktion der Gewächse der Záhorie-Tiefebene. Biol. Práce 11. No. 3, 1–100.

Kriván, P. 1960: A Duna ártéri szinlőinek kronológiája. [Chronologie der alluvialen Donauterrassen in Ungarn]. Földt. Közl. 90. 56–72.

Lissizina, N. G. 1953: Neue Angaben über die Vegetationsdecke der russischen Ebenein spät- und postglazialer Zeit. Nachr. Akad. Wiss. UdSSR, geogr. ser. 2. 42–49.

Miháltz, I., Miháltz-Faragó, M. 1965: Attempt at a pollen chronology in Quaternary fluviatile deposits. Acta Biol. Szeged, 11. 295–299.

Mikkelsen, V. M. 1949: Praesto Fjord. The development of the postglacial vegetation and a contribution to the history of the Baltic Sea. Dansk Bot. Ark. 13. No. 5, 1–171.

Morrison, M. E. S. 1959: Evidence and interpretation of „landnam" in the North-East of Ireland. Bot. Notis. 112. 185–203.

Pálinkás, Gy. 1955: Szőlészeti és borászati zsebkönyv. [Handbook of ampelology and oenology]. Mezőgazdasági Kiadó, Budapest.

Praglowski, H. J. 1962: Notes on the pollen morphology of Swedish trees and shrubs. Grana Palynol. 3. No. 2, 45–65.

Ralska-Jasiewiczowa, M. 1966: Bottom Sediments of the Mikolajki Lake (Masurian Lake District) in the Light of Palaeobotanical Investigations. Acta Palaeobot. 7. No. 2, 1–118.

Samuelsson, C. 1934: Die Verbreitung der höheren Wasserpflanzen in Nordeuropa. Beih. Bot. Centralbl. 47. 111–176.

Simon, T. 1957: Die Wälder des nördlichen Alföld. [The forests of North Great Plain.] Akadémiai kiadó, Budapest.

Smith, A. C. 1961: The Atlantic-Subboreal transition. Proc. Linnean Soc. London, 172 Sess., 1959–1960, 38–49.

Soó, R. 1926: Die Entstehung der ungarischen Puszta. Ungar. Jahr. 6. 258–276.

Soó, R. 1929: Die Vegetation and Entstehung der ungarischen Puszta. J. Ecology 17. 329–350.

Soó, R. 1931: A Magyar Puszta fejlődéstörténetének problémája. [The Vegetation and the Development of the Hungarian "Puszta"]. Földr. Közl. 59. 1–17.

Soó, R. 1940: Vergangenheit und Gegenwart der pannonischen Flora und Vegetation. Nova Acta Leopoldina 9. No. 56, 1–49.

Soó, R. 1957: Systematische Übersicht der pannonischen Pflanzengesellschaften I. Acta Bot. Acad. Sci. Hung. 3. 317–373.

Soó, R. 1958: Die Wälder des Alföld. Acta Bot. Acad. Sci. Hung. 4. 351–381.

Soó, R. 1959: Entwicklungsgeschichte der Pflanzenwelt Ungarns. Phyton 8. 114–129.

Soó, R. 1964: A Magyar Flóra és Vegetáció Rendszertani-Növényföldrajzi Kézikönyve I. [Synopsis systematico-geobotanica florae vegetationisque Hungariae]. Akadémiai Kiadó, Budapest.

Soó, R., Jávorka, S. 1951: A Magyar Növényvilág Kézikönyve I–II. [The Handbook of the Hungarian Flora]. Akadémiai Kiadó, Budapest.

Stieber, J. 1957: A hazai felső-pleisztocénből származó faszénmaradványok anthrakotomiai vizsgálata. Kandidátusi disszertáció, Budapest. Kézirat.

Szafer, W. 1954: Pliocene flora from the vicinity of Czersztya (West Carpathians), and its relationship to the Pleistocene. Inst. Geol. Prace **11.** 1–230.

Szczepanek, K. 1961: The history of the Late Glacial and Holocene vegetation of the Holy Cross Mountains. Acta Palaeobot. **2.** No. 2, 1–45.

Terpó, A. 1962: Adatok a hazai vadontermő Vitisek ismeretéhez. [Some data of the knowledge of native Vitis]. Kert. Szől. Főisk. Évk. **26.** 147–161.

Troels-Smith, J. 1960: Ivy, mistletoe and elm. Climate indicators – fodder plants. Danm. Geol. Unders. IV. R. No. 4, 1–32.

Turner, J. 1962: The Tilia decline: an anthropogenic interpretation. New Phytol. **61.** 328–341.

Turner, J. 1964: The anthropogenic factor in vegetational history. New Phytol. **63.** 73–90.

Vozáry, E. 1957: Pollenanalytische Untersuchung des Torfmoore „Nyírestó" im Nordosten der ungarischen Tiefebene (Alföld). Acta Bot. Acad. Sci. Hung. **3.** 123–134.

Walter, H. 1954: Einführung in die Phytologie III. Grundlagen der Pflanzenverbreitung. 2. Arealkunde. Ulmer Verlag, Stuttgart.

Wasylikowa, K. 1964: Vegetation and climate of the Late Glacial in Central Poland based on investigations made at Witów near Leczyca. Biul. Perygl. **13.** 261–417.

Wendelberger, G. 1954: Steppen, Trockenrasen und Wälder des pannonischen Raumes. Angw. Pflanzensoz. **1.** 573–634.

Wendelberger, G. 1956: Die Waldsteppen des pannonischen Raumes. Veröff. Geobot. Inst. Rübel in Zürich, H. 35, 77–113.

West, R. G. 1964: Inter-relations of ecology and Quaternary palaeobotany. J. Ecol. **52.** (Suppl.), 47–57.

van Zeist, W. 1959: Studies on the post-Boreal vegetational history of south-eastern Drenthe (Neth.). Acta Bot. Neer. **8.** 156–184.

Zólyomi, B. 1931: A Bükkhegység környékének Sphagnum lápjai. [Vegetationsstudien an den Sphagnummooren um das Bükkgebirge in Mittelungarn]. Bot. Közl. **28.** 89–121.

Zólyomi, B. 1946: Természetes növénytakaró a tiszafüredi öntözőrendszer területén. Öntözésügyi Közl. 7–8. 62–74.

Zólyomi, B. 1953: Die Entwicklungsgeschichte der Vegetation Ungarns seit dem letzten Interglazial. Acta Biol. Acad. Sci. Hung. **4.** 367–430.

Zólyomi, B. 1958: Budapest és környékének természetes növénytakarója. In: Budapest természeti képe. [Die natürliche Vegetation von Budapest und seiner Umgebung In: Naturbild von Budapest]. Akadémiai Kiadó, Budapest.

Zólyomi, B. 1964: Pannonische Vegetationsprobleme. Verh. Zool. Bot. Ges. Wien. **103–104.** 144–151.